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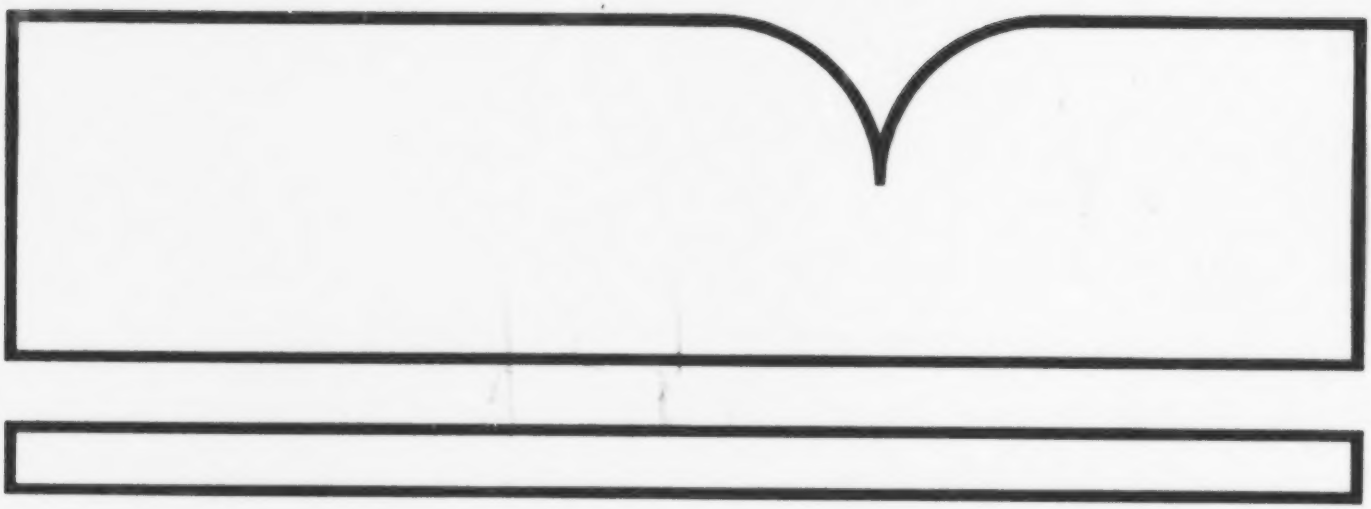

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PERSISTENCE IN MODEL ECOSYSTEMS

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FOREWORD

Environmental protection efforts are increasingly directed towards preventing adverse health and ecological effects associated with specific compounds of natural or human origin. As part of this Laboratory's research on the occurrence, movement, transformation, impact, and control of environmental contaminants, the Environmental Systems Branch studies complexes of environmental processes that control the transport, transformation, degradation, and impact of pollutants and other materials in soil and water and assesses environmental factors that affect water quality.

Mathematical models are being developed and used increasingly by environmental scientists as tools for understanding the behavior of pollutants in water. Some of these models take the form of differential equations that describe the growth-decay rate of a substance or an organism constituting a component of the environmental system being modeled. This report presents a technique for evaluating the solutions of these differential equations.

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ABSTRACT

Mathematical models aid in understanding environmental systems and in developing testable hypotheses relevant to the fate and ecological effects of toxic substances in such systems. Within the framework of microcosm or laboratory ecosystem modelling, some differential equation models, in particular, become tractable to mathematical analysis when the focus is on the problem of persistence. In this report a hierarchy of microcosm-related models, the top level of which contains a nutrient-producer-grazer food chain, and general food chains are analyzed for persistence. The results, which take the form of inequalities involving model parameters, specify necessary conditions and sufficient conditions for continued presence of the model components throughout indefinite time intervals. These results can serve as a basis for preliminary evaluations of model performance.

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SECTION 1

INTRODUCTION

Certain mathematical models of environmental systems take the form of differential equations, with each equation describing the growth-decay rate of a substance or an organism constituting a component of the environmental system modelled. In general the differential equations are nonlinear and exact solutions in terms of elementary functions are impossible to obtain. In this case, the mathematics appropriate to analyzing such models involves approximation techniques, of which there are two fundamental types. One method is to directly approximate the solutions; algorithms for generating numerical solutions by computer are used to implement this method. This approach is effective if parameter values in the model are reasonably well-known and if interest is focused on solutions corresponding to limited sets of initial values for the model components. The second method essentially deals with approximating the differential equations and obtaining information about the solutions by comparison with solutions of the (hopefully) simpler approximating system. The technique here consists of constructing auxiliary functions and differential inequalities and has an algebraic character. The results are qualitative rather than quantitive and, although less specific, nevertheless are valid over wider ranges of parameter and initial values. The work reported on here exemplifies this second method of analysis.

Persistence in mathematical models of ecosystems is the analogue for survival of organisms and continued presence of substances in the systems modelled and hence is a very relevant aspect of such models in terms of the mission of the Environmental Protection Agency. In the context of differential equation models, the problem of determining persistence can be approached by the qualitative techniques of analysis described above. The results are formulated as ranges of model parameter values for which persistence holds.

SECTION 2

DESCRIPTION OF RESEARCH

GENERAL SETTING

The research reported on here deals with the mathematical analysis of models of ecological subsystems. The mathematical models take the form of a system of ordinary differential equations

$$x_i' = f_i(x_1,\ldots,x_n) \quad i = 1,\ldots,n \tag{1}$$

$$' = \frac{d}{dt}$$

where the state variable $x_i(t)$ represents the density of the i th component substance or organism of the ecological subsystem modelled at time t ; the i th equation in (1) gives the rate of growth or decay of the i th component as a function of all state variables at time t . Of interest are solutions $(x_1(t),\ldots,x_n(t))$ of (1) which remain in the feasible region

$$R_+^n = \{(x_1,\ldots,x_n): x_i \geq 0 , \text{ all } i\} ,$$

and in particular solutions that at least originate in the interior of the feasible region

$$R_+^{n,o} = \{(x_1,\ldots,x_n): x_i > 0 , \text{ all } i\} .$$

Under mild assumptions that are consistent with the applications on the functions f_i , for any initial value $(x_1^o,\ldots,x_n^o)$ in R_+^n , there exists a unique solution $(x_1(t),\ldots,x_n(t))$ of (1) which satisfies $x_i(0) = x_i^o$, for each i , and which is bounded. The analysis of (1) focuses on the qualitative property of persistence. In the setting described above persistence is defined by

$$\limsup_{t\to\tau} x_i(t) > 0 \quad i = 1,\ldots,n , \ \tau \in (0,\infty] \tag{2}$$

for each solution $(x_1(t),\ldots,x_n(t))$ of (1) with initial value

$(x_1(0),\ldots,x_n(0))$ in $R_+^{n,o}$. That is, persistence means that no component of a solution which initially has all components positive can vanish over any definite or indefinite time interval. Failure of persistence (extinction) consequently indicates that there is some solution of (1) with positive initial densities $x_i(0)$, $i = 1,\ldots,n$ which exhibits the behavior $x_j(t) \to 0$ as $t \to \tau$, for some integer j, $1 \leq j \leq n$ and some $\tau \in (0,\infty]$. A consequence of persistence in systems of the form (1), implied by the general theory of dynamical systems (Nymetskii and Stepanov, 1960), is that every solution $(x_1(t),\ldots,x_n(t))$ with initial value in $R_+^{n,o}$ must approach an equilibrium or a recurrent (oscillatory type) solution contained in $R_+^{n,o}$.

MICROCOSM RELATED MODEL

Microcosms or laboratory ecosystems have become an important tool in environmental system analysis, and a hierarchy of related hypothetical mathematical models has been proposed to investigate the complexities of structure in such ecosystems (Lassiter, 1978). The simplest of these models (the chemostat) consists of two components, a nutrient resource (N) and a producer (P). The next level (cycling) includes components for organic material (O) derived from the producer and a decomposer (D) which mineralizes O back to nutrient form. The most complicated model (food chain) in the hierarchy adds a grazer (Z) to the cycling model; this model has the form

$$N' = \frac{N_0}{\theta} - N\left(\frac{1}{\theta} + \mu_P \frac{P}{k_{NP}+N}\right) + \left(\frac{1}{Y_{ND}} - 1\right)\mu_D\left(\frac{O}{k_{OD}+O}\right)D \tag{3a}$$

$$P' = P\left(-\frac{w_P}{\theta} - d_P + \mu_P \frac{N}{k_{NP}+N} - \frac{\mu_Z}{Y_{PZ}} \frac{Z}{k_{PZ}+P}\right) \tag{3b}$$

$$D' = D\left(-\frac{w_D}{\theta} - d_D + \mu_D \frac{O}{k_{OD}+O}\right) \tag{3c}$$

$$O' = O\left(-\frac{w_O}{\theta} - \frac{D}{Y_{ND}} \frac{D}{k_{OD}+O}\right) \tag{3d}$$

$$+ d_P P + d_D D + Z\left(d_Z + \left(\frac{1}{Y_{PZ}} - 1\right)\mu_Z \frac{P}{k_{PZ}+P}\right)$$

$$Z' = Z\left(-\frac{w_Z}{\theta} - d_z + \mu_Z \frac{P}{k_{PZ}+P}\right) \tag{3e}$$

where $' = \frac{d}{dt}$

The cycling model consists of the first four equations with Z set to zero; this system will be denoted (4a)-(4d). If in addition O and D are set equal to 0, the first two equations above, labelled in this case (5a) and (5b), constitute the chemostat. The parameters

nutrient input: N_0

maximum growth rates: μ_P, μ_D, μ_Z

death rates: d_P, d_D, d_Z

half saturation constants: k_{NP}, k_{OD}, k_{PZ}

yield coefficients: Y_{NP}, Y_{PZ}

washout coefficients: w_P, w_D, w_O, w_Z

retention time: θ

are assumed to be positive constants with yield coefficients less than one and washout coefficients not exceeding one.

What follows summarizes the main results in a manuscript (Gard, 1979) submitted for publication. By considering the new variable $S = N + P + O + D + Z$, it was shown that all solutions in the feasible region are bounded and that certain necessary conditions for persistence are immediate, namely

$$\mu_P \theta - w_P - d_P \theta \geq 0$$

$$\mu_D \theta - w_D - d_D \theta \geq 0$$

$$\mu_Z \theta - w_Z - d_Z \theta \geq 0$$

The principal results obtain a set of five functions $N_1,\ldots,N_5$ of the model parameters such that for persistence in

(a) the chemostat ((5a), (5b)), $N_0 > N_1$ is necessary and sufficient

(b) the cycling model ((4a) - (4d)), $N_0 \geq N_2$ is necessary and $N_0 > N_2$ is sufficient, and

(c) the food chain ((3a) - (3e)), the following conditions are necessary:

(i) $N_0 \geq N_3$, $\bar{N}_2 \leq N_0 < N_2$, or $\bar{N}_2 < N_0 \leq N_2$

(ii) If, furthermore $N_0 > N_4$, then either $\beta \leq 0$ or $\beta > 0$, $\mu_P - (w_P + (\alpha + d_P)\theta) > 0$ and $N_0 \geq N_5$.

The functions N_i and β are given by:

$$N_1 = \eta_{NP}$$

$$N_2 = w_O\left(\frac{w_P}{d_P\theta} + 1\right)\eta_{OD} + \eta_{NP} \qquad \bar{N}_2 = (w_P + d_P\theta)\eta_{PZ} + \eta_{NP}$$

$$N_3 = \eta_{NP} + \frac{(w_P\alpha + d_P\theta w_D Y_{ND})\eta_{PZ} + (w_D + d_D\theta)(1-Y_{ND})w_O\eta_{OD}}{\alpha}$$

$$N_4 = \eta_{NP}\left(1 + \frac{\mu_P\theta\eta_{PZ}}{k_{NP}+\eta_{NP}}\right)$$

$$N_5 = [w_P + (\beta + d_P)\theta]\left[\eta_{PZ} - \frac{k_{NP}\{w_P + (\beta+d_P)\theta\}}{\mu_P\theta\{\mu_P\theta - [w_P + (\beta+d_P)\theta]\}}\right]$$

where $\eta_{AB} = \dfrac{k_{AB}(w_B+d_B\theta)}{\mu_B\theta - (w_B+d_B\theta)}$ $\qquad$ AB = NP, PZ, OD

and

$$\alpha = w_D + d_D\theta(1 - Y_{ND})$$

$$\beta = \frac{\mu_Z(w_O\eta_{OD} - d_P\theta\eta_{PZ})}{(k_{PZ}+\eta_{PZ})(w_Z[1-Y_{PZ}]+d_Z\theta)}$$

For the most complex of these models (3(a) - 3(e)) a sufficient condition for persistence was not determined. A conjecture is that $N_0 > \max\{N_3, N_4, N_5\}$ would imply persistence. The conjecture would be true if it could be shown that subsystems of the model corresponding to $D = 0$ and $Z = 0$ admit no solutions of oscillatory type.

The mathematical technique here consists of determining feasibility of equilibria, ruling out periodic solutions, and carrying out an eigenvalue analysis of the equilibria in the boundary of the feasible region.

FOOD CHAIN MODELS

The ability to predict ecological effects of introducing a toxic substance into a food chain subsystem would complement the toxic substance fate studies being carried out by the U.S. Environmental Protection Agency. In what follows results concerning persistence in various mathematical models of food chains are described. Lotka-Volterra food chain results (Gard

and Hallam, 1979) are extended to cases of other and more general type interactions (Gard, 1980 a,b) and to cases where omnivory and external supplementation of the food source or an intermediate predator is allowed (Gard, 1980 c). Lotka-Volterra food chains have the form

$$\begin{aligned} x_1' &= x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\ x_i' &= x_i(-a_{i0} + a_{i,i-1}x_{i-1} - a_{i,i+1}x_{i+1}), \quad 1 < i < n \\ x_n' &= x_n(-a_{n0} + a_{n,n-1}x_{n-1}) \end{aligned} \tag{6}$$

where the a_{ij} are positive constants, In this case persistence is characterized by the sign of a single parameter

$$\mu = a_{10} - \frac{a_{11}}{a_{21}}\left[a_{20} + \sum_{j=2}^{k}\left(\prod_{i=2}^{j}\frac{a_{2i-2,2i-1}}{a_{2i,2i-1}}\right)a_{2j,0}\right] - \sum_{j=1}^{\ell}\left(\prod_{i=1}^{j}\frac{a_{2i-1,2i}}{a_{2i+1,2i}}\right)a_{2j+1,0}$$

where $k = \begin{cases} \frac{n}{2} & \text{if } n \text{ is even} \\ \frac{n-1}{2} & \text{if } n \text{ is odd} \end{cases}$ and $\ell = \begin{cases} \frac{n}{2} - 1 & \text{if } n \text{ is even} \\ \frac{n-1}{2} & \text{if } n \text{ is odd} \end{cases}$.

If μ is positive, persistence holds for (6), and if μ is negative persistence fails (Gard and Hallam, 1979). Holling-type food chains are obtained if the interaction constants a_{ij} in (6) are replaced by density dependent functions of the form $a_{ij}/(b_i+x_i)$. In particular, taking $n = 3$ and replacing the interaction coefficients a_{12} and a_{21} in (6) by $a_{12}/(b_1+x_1)$ and $a_{21}/(b_1+x_1)$, respectively, results in a Holling model; here, μ_H positive is a sufficient condition and ν_H nonnegative is a necessary condition for persistence, where

$$\mu_H = a_{10} - \left[\frac{ba_{11} + \frac{a_{12}}{ba_{32}}a_{30}}{a_{21}-a_{20}}\right]a_{20} - \frac{a_{12}}{a_{32}}a_{30} \qquad (a_{21} - a_{20} > 0)$$

$$\nu_H = a_{10} - \left[\frac{ba_{11} - \frac{a_{12}}{ba_{32}}\left(1 - \frac{a_{20}}{a_{21}}\right)a_{30}}{a_{21}-a_{20}}\right]a_{20} - \frac{a_{12}}{a_{32}}a_{30}$$

(Gard, 1980 a). For models with general interactions (for $j \neq 0$, replace a_{ij} and a_{ji} by $a_{ij}g_i(x_i)$ and $a_{ji}g_i(x_i)$ respec-

tively, $i < j$) that are bounded on a compact interval to the right of zero

$$0 < m_i \leq g_i(x_i) \leq M_i, \quad x \in [0, \bar{x}_i]$$

where $\bar{x}_i$ is determined in terms of the a_{ij}, parameters and μ and ν can be determined whose positivity and nonnegativity respectively constitute sufficient and necessary conditions for persistence (Gard, 1980 b); μ and ν are algebraic expressions involving the a_{ij}, m_i and M_i. In each of the above situations the fact that persistence is equivalent to top predator persistence facilitated the analysis. This property does not hold when the possibilities of predators feeding on multiple trophic levels and intermediate predators being externally supplemented are considered. As in the case of more than one species per trophic level (Hallam, Svoboda, and Gard, 1979) several parameters are required to specify full system persistence. However, top predator persistence remains reasonably tractable. The food chain exhibiting general omnivory has the form

$$\left.\begin{aligned} x_1' &= x_1\left(a_{10} - \sum_{i=1}^{n} a_{ij}x_i\right) \\ x_j' &= x_j\left(-a_{j0} + \sum_{i=1}^{j-1} a_{ji}x_i - \sum_{i=j+1}^{n} a_{ji}x_i\right), \quad 1 < j < n \\ x_n' &= x_n\left(-a_{n0} + \sum_{i=1}^{n-1} a_{ni}x_i\right) \end{aligned}\right\} \qquad (7)$$

The a_{ij} are assumed positive, but may be functions of time t and the component densities x_i. In the latter case the functions a_{ij} are assumed continuous and bounded, i.e.

$$0 < m_{ij} \leq a_{ij}(t,x) \leq M_{ij}$$

for some constants m_{ij} and M_{ij}, and all t and x, or a_{ij} vanishes identically in which case $a_{ji}(t,x) = 0$ all t and x is also required. The main result is stated in terms of an $n-1 \times n-1$ matrix A and an $n-1$ vector b defined by

$$A = \begin{pmatrix} m_{21} & m_{31} & m_{41} \cdots & m_{n1} \\ 0 & m_{32} & m_{42} \cdots & m_{n2} \\ -M_{23} & 0 & m_{43} \cdots & m_{n3} \\ \vdots & & & \\ -M_{2,n-1} \cdots -M_{n-2,n-1} & & 0 & m_{n,n-1} \end{pmatrix} \qquad b = \begin{pmatrix} M_{11} \\ M_{12} \\ \cdot \\ \cdot \\ \cdot \\ M_{1,n-1} \end{pmatrix}$$

Persistence for the top predator holds if

$$\mu(r) = m_{10} - \sum_{i=2}^{n} r_i M_{i0} > 0$$

for some vector $r = (r_2,\ldots,r_n)^T$ with $r_i > 0$, $i = 2,\ldots,n$ which satisfies the vector matrix inequality $Ar \geq b$. (Gard, 1980 c). The model analogue for supplementing an intermediate predator is obtained by adding a positive function $a_k(t,x)$ to the right hand side of the k th equation in (7), where $1 < k < n$. The top predator persistence criterion this time (Gard, 1980 c) is

$$\mu_k(r) = 4r_k m_k \left[\sum_{i=k+1}^{n} r_i m_{ik} - \sum_{i=2}^{k-1} r_i M_{ik} - M_{1k} \right]$$

$$- \left[m_{10} - \sum_{i=2}^{n} r_{i0} M_{i0} \right]^2 > 0$$

where $r = (r_2,\ldots,r_n)^T$ satisfies the same conditions as in the omnivory result above, and m_k is a (positive) lower bound for a_k.

The principal technique used to obtain all the results described in this section involves the construction of an auxiliary function $\rho(x_1,\ldots,x_n;r_1,\ldots,r_n)$ with the property that ρ tends to zero if and only if some x_i approaches zero. The total time derivative

$$\dot{\rho}(x) = \frac{d\rho(x(t))}{dt}$$

of ρ along solution paths $x(t)$ can be expressed in terms of the right hand sides of (7). The assumptions in each one of the results cited above allow choices of the free parameters $r_1,\ldots,r_n$ so that it is possible to show

$$\dot{\rho}(x) > 0$$

at least for sufficiently large values of t. This guarantees that ρ cannot vanish and hence x_n cannot approach zero, i.e. persistence for the top trophic level predator holds.

SECTION 3

SUMMARY

The mathematical analysis focusing on persistence in differential equation models of current and future potential interest to the Environmental Protection Agency results in criteria taking the form of inequalities involving model parameters. For the five-component, microcosm-related model and its subsystems, these results are expressed in terms of threshold values for the nutrient input rate. In the case of the food chain models, positivity of weighted sums of the intrinsic growth-decay rates constitute the conditions for persistence. Generally, the nutrient input level, the intrinsic growth rate of the food source, or the rate of supplementation of intermediate predator being sufficiently large guarantees persistence. The methods used consist of approximating the differential equations; in particular, linearization and the auxiliary function-comparison principle techniques are the main tools employed from the qualitative theory of ordinary differential equations.

In each of these models, it has been shown that solutions are bounded. A consequence of persistence for autonomous (right hand side of equations independent of t explicitly) systems, in this case, is that any solution with positive initial values must approach asymptotically either an equilibrium or a solution of oscillatory type in the interior of the feasible region. Furthermore, and possibly most significant, is the fact that persistence implies the existence of a recovery mechanism in the model. Solutions exhibiting small component densities at some time t tend to equilibrium or oscillatory type stable density configurations in the interior of the feasible region. That these models do not take into account stochastic effects contributes to this result.

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